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Performance of younger and older adults in lateralized right and left hemisphere
asymmetry tasks supports the HAROLD model

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Abstract

The population of industrialized societies has increased tremendously over the last century, raising the question on how an enhanced age affects cognition. The relevance of two models of healthy aging are contrasted in the present study that both target the functioning of the two cerebral hemispheres. The right hemi-aging model (RHAM) assumes that functions of the right hemisphere decline before those of the left hemisphere. The Hemispheric Asymmetry Reduction in Older Adults (HAROLD) Model suggests that the contralateral hemisphere supports the normally superior hemisphere in a given task resulting in a reduced hemispheric asymmetry overall. In a mixed design, 20 younger and 20 older adults performed both a task assessing a left (lateralized lexical decisions) and a right (sex decisions on chimeric faces) hemisphere advantage. Results indicated that lateralized performance in both tasks was attenuated in older as compared to younger adults, in particular in men. These observations support the HAROLD model. Future studies should investigate whether this reduced functional hemispheric asymmetry in older age results from compensatory processes or from a process of de-differentiation.

Key words: aging, hemispheric asymmetry, laterality, right hemi-aging model (RHAM) chimeric faces, lexical decisions, perceptual bias.

Introduction

The life expectancy in industrialized countries has increased tremendously in the last century. The average age for females has risen from 69 years in 1950 to an average age of 81 years in 2009 and for males from 64 years in 1950 to an average of 74 years in 2009 (<http://www.prb.org/pdf09/64.3highlights.pdf>). While this longevity allows most individuals to enjoy activities well into their 70ies and 80ies, this age trend also raises many yet unsolved questions and challenges, among others about cognitive decline and cognitive compensation (Park & Reuter-Lorenz, 2009). For instance, older adults perform more poorly than younger adults in a variety of cognitive tasks, including those on perception, attention, and memory (Babcock & Salthouse, 1990; Craik & Salthouse, 2000; Gick, Craik, & Morris, 1988; Li, Lindenberger, & Sikstrom, 2001). However, whereas some healthy older adults show a reduction in performance in many cognitive tasks, others perform as well as or even better than younger adults (Christensen et al., 1999). It has been assumed that decreased cognitive functioning is related to an increased fatigue of neuronal resources (Reuter-Lorenz & Cappell, 2008).

During aging, the human brain undergoes a series of deleterious changes, including gray and white matter atrophy, synaptic degeneration, blood flow reductions, and neurochemical alterations (Cabeza, 2001; Raz, 2000). Yet, such changes might differ between individuals, potentially explaining that neuronal fatigue progresses more rapidly in some older adults than others (Reuter-Lorenz & Cappell, 2008). Another explanation

could be that the brains of high-performing older adults compensate for age-related neural decline by means of reorganization and changes in functional connectivity between brain areas (Cabeza, Anderson, Locantore, & McIntosh, 2002), in particular within prefrontal structures (Park & Reuter-Lorenz, 2009). Two models on the cerebral markers of healthy aging have been presented with the first being the right hemi-aging model (RHAM) (Albert & Moss, 1988; Brown & Jaffe, 1975), and a later model being the Hemispheric Asymmetry Reduction in Older Adults (HAROLD) Model (Cabeza, 2002). Both models assume that the human brain compensates for age-related changes in neuronal mechanisms that affect cognitive functioning by methods of reorganization and changes on functional connectivity (see also Cabeza, 2001; Grady et al., 1994; Raz, 2000; Tsujii, Okada, & Watanabe, 2010). As will be shown, it is common to both models that they focus on changes in common patterns of functional hemispheric asymmetry.

The RHAM predicts that age related cognitive decline is more pronounced on cognitive functions associated with the right hemisphere (e.g. spatial processing, visual face processing). The model assumes a greater decline of right hemispheric functioning given the right hemisphere's stronger sensitivity to aging due to a smaller gray/white matter ratio (Good et al., 2001; Gur et al., 1980; Pujol et al., 2002). The HAROLD model assumes that a more bilateral pattern of hemispheric functioning in older as compared to younger adults might reflect functional compensation of the contralateral hemisphere assisting the normally superior hemisphere during a given task. This is based on findings

from behavioural and functional neuroimaging studies showing that frontal activity during cognitive performance in the domains of episodic memory encoding and retrieval, semantic memory retrieval, working memory, perception, and inhibitory control tends to be less lateralized in older compared to younger adults (see Cabeza, 2002; Hommet, Destrieux, Constans, & Berrut, 2008 for overviews). A relatively recent qualitative meta-analysis on findings from imaging studies hinted at a particularly affected right dorsal and anterior prefrontal cortex (Rajah & D'Esposito, 2005). Beyond observations of changes in functional hemispheric asymmetries, these changes seem cognitively advantageous to the older adults; additional contralateral hemispheric involvement has been associated with relative enhanced cognitive functioning in older adults (Cabeza et al., 2002; Reuter-Lorenz et al., 2001; Tsujii et al., 2010), conclusions that were also inferred from studies using lateralized divided half-field paradigms (Cherry, Adamson, Duclos, & Hellige, 2005; Reuter-Lorenz, Stanczak, & Miller, 1999).

In divided half-field paradigms, stimuli are presented briefly (around 150ms) to the right and left half-field (e.g. visual, auditory). This procedure exploits the fact that the respective sensory pathways are partially crossed so that a stimulus presented to the right of centre (right visual field, RVF) is first processed by the left hemisphere, and a stimulus presented to the left of centre (left visual field, LVF) is first processed by the right hemisphere. By exposing participants to different stimulus material (e.g. language material, rotated figures, faces), the advantage of one over the other hemisphere can be

assessed. Most reliable, for instance, are findings on the left hemisphere's advantage for language (Hugdahl, 2000); performance (accuracy, response latencies) is commonly superior for words presented to the RVF / right ear than to the LVF / left ear (Hugdahl, 2011; Kimura, 1961; Michael, 2009; Mishkin & Forgays, 1952). Another common hemispheric asymmetry task taps into the right hemisphere's advantage for visual face processing, i.e. performance is commonly biased towards the LVF (Butler & Harvey, 2006; Schwartz & Smith, 1980; Voyer, Voyer, & Tramonte, in press). These biases support functional hemispheric asymmetries formerly described from neuropsychological patient studies (e.g. Broca, 1865; Hoff & Pötzl, 1937; Kimura, 1961 for some early accounts).

To the present study, such lateralized half-field paradigms are of major interest, because they can assess functional hemispheric asymmetries non-invasively (Hunter & Brysbaert, 2008), and are easily performed in the laboratory. Moreover, such paradigms should be sensitive to assess the relevance of the RHAM and the HAROLD model, because more than one task can be assessed within the same participant, i.e. one task measuring the hemispheric advantage of the left hemisphere and one measuring the hemispheric advantage of the right hemisphere (see e.g. Borod & Goodglass, 1980; Hausmann, Gunturkun, & Corballis, 2003; Obler, Woodward, & Albert, 1984). If performance for only one task would be investigated, the two models could not be contrasted (e.g. Butler & Harvey, 2008).

Some previous studies inferred on the relevance of the RHAM and HAROLD model using such paradigms, many using lateralized matching tasks. Reuter-Lorenz, Stanczak, and Miller (1999), for example, performed a letter matching task with varying complexity in 24 older and 24 younger adults. In this task, two letter stimuli were presented either uni- or bilaterally. Irrespective of age, participants showed a bilateral visual field advantage in medium and high, but not low complexity conditions. Interestingly, this bilateral advantage was already present for older adults in the low complexity condition (see also Reuter-Lorenz & Cappell, 2008) indicating that an enhanced interhemispheric coordination is already necessary for easier tasks in older adults (Banich, 1998). This was taken as support for the HAROLD model (see also Smith-Conway, Chenery, Angwin, & Copland, 2012 for a similar conclusion from the performance of 13 older adults in a lateralized semantic priming task).

A variety of studies inferred that their results support the RHAM model. In a cross-sectional study, Goldstein and Shelly (1981) tested the neuropsychological functioning of 1247 participants, divided into six age groups (20's-70's). The older as compared to younger age group yielded a stronger decline in task performances, but this decline was more pronounced for tasks targeting the right than left hemisphere (see also Hommet et al., 2008). Cherry et al. (2005), comparable to the study by Reuter-Lorenz et al. (1999), performed letter matching tasks, i.e. a physical and name identity task. Again, the more

complex the task (the harder name identity task as compared to the easier physical identity task), the more the 20 older as compared to 30 younger adults yielded a bilateral advantage. The older adults, however, did not show the overall right hemisphere advantage observed in younger adults. In another study, digit recall in a dichotic listening paradigm became worse with increasing age (112 individuals separated into 4 age groups), but this decrement was particularly pronounced for the left ear (Clark & Knowles, 1973). Further independent studies using various lateralized tasks also reported on evidence in support of the RHAM (object discrimination task in 16 younger and 16 older individuals: Gerhardstein, Peterson, & Rapcsak, 1998).

When considering the findings on lateralized half-field paradigms, it seems that more studies are in favour of the RHAM model. It needs to be noted, however, that additional studies found no difference in lateralization pattern between younger and older populations, whether testing 120 men of different ages on verbal (left hemisphere advantage) and melodic (right hemisphere advantage) material (Borod & Goodglass, 1980), or whether testing 32 younger women and 32 older women on lateralized tasks in which they needed to compute visual-spatial relations (Hoyer & Rybash, 1992). Also, using a letter and a face matching task, no difference in lateralization was observed when comparing performances between three age groups (16 men and 16 women in each group) (Obler et al., 1984). Finally, testing three lateralized paradigms, Hausmann et al. (2003) found that findings from a face recognition task, and a word and figural

comparison task performed in 50 younger and 42 older adults would neither support the HAROLD model nor the RHAM. Moreover, participants' sex interacted with lateralized task performance, at least in the figural comparison task.

Given the inconsistency in the previous literature and the multitude of tasks employed, we here performed a study on younger and older adults on both a right and left hemisphere asymmetry task. Important to the present study, performance in both tasks has been assessed in an independent sample with results from the two tasks complementing each other (Herzig, Tracy, Munafò, & Mohr, 2010). One task assessed the left hemisphere's advantage for language using a lateralized lexical decision task (see also Dutta & Mandal, 2002; Mishkin & Forgays, 1952) and the other task assessed the right hemisphere's advantage for visual face processing by assessing sex decisions for chimeric faces (see also Butler & Harvey, 2006; Dutta & Mandal, 2002). In the lateralized lexical decision task, letter strings are shortly presented to the LVF and RVF. Information presented to the RVF is initially processed by the left hemisphere, and vice versa, information presented to the LVF is initially processed by the right hemisphere. Hence, performance is commonly superior for RVF than LVF word recognition (Bourne, 2006; Hunter & Brysbaert, 2008 for overviews on best practice when using these procedures). In the chimeric face task, faces that differ for the left (e.g. male) and right side (e.g. female) are briefly presented. Thus, the left face is initially processed by the right hemisphere and the right face by the left hemisphere. Healthy participants usually

show a bias towards processing the left side of the face pointing to a right hemisphere advantage in visual face processing (Butler & Harvey, 2006; Dutta & Mandal, 2002).

In sum, we here tested 20 older and 20 younger adults in both a right and left hemisphere asymmetry task to investigate whether results would rather support the HAROLD or the RHAM model. If the HAROLD model is more likely to be true, we would expect both a reduced RVF advantage in the lateralized lexical decision task and a reduced left face bias in the facial decision task in older as compared to younger adults. If the RHAM model is more likely to be true, we would expect such age group differences for the chimeric face task, with a potential stronger RVF advantage in the lexical decision task.

Method

Participants

Twenty older (10 men) and 20 younger (10 men) volunteers were recruited from the general population. Comparable to previous studies (Cherry et al., 2005; Reuter-Lorenz et al., 1999), older adults (age always in years) were 60 and older (mean ($\pm SD$) age 64.8 ± 4.76 , range 60 -75), and the younger adults were 30 years and younger (26.1 ± 4.53 , range 18-30). This age difference was significant according to an independent t-test ($t(39) = 18.735$, $p < .001$). All participants were native English speakers, and had normal or corrected-to-normal vision. Moreover, all participants were right-handed according to the 12-item Edinburgh handedness inventory (Oldfield, 1971). This inventory assesses

preference for use of right, left, or either hand for various activities, such as opening a box or striking a match. Right-hand preference receives a score of one point per question, left hand zero, and either 0.5. Responses are summed and a mean taken to give a score between zero and one. Participants with a score of 0.75 or above were considered to be right-handed (e.g. Mohr & Leonards, 2007) and included in the study, participants with a score below 0.75 were excluded.

The older adult group consisted of residents in a warden controlled sheltered housing scheme, and recruited with the approval from the sheltered housing officer in charge of the scheme. The housing officer also guaranteed that no participant with known cognitive impairments was invited for testing. Accordingly, all older adults were neurologically intact with no known history of cognitive dysfunction. The younger adults were recruited through personal contact, and matched in age and education with the older adults, i.e. all were educated to secondary school level and had not been to university. None of the younger adults reported any neurological or psychological illnesses by self-report. The study has been approved by the local ethics committee, and all participants provided written informed consent prior to testing.

Lateralized Tasks

Common procedure to both tasks was that participants were sat centrally 57cm from the computer screen (eye-screen distance). The keyboard was centrally placed in front of the

participant so that the response keys were to the right and left of the body midline.

Stimuli were presented on a computer screen using the experimental run system E-Prime (© Psychology Software Tools) with a monitor display refresh rate of 60Hz.

Lateralized Lexical Decision Task

Participants were presented with an English version (Herzig et al., 2010) of the lateralized lexical decision task used by Mohr, Krummenacher *et al.* (2005) before. The stimulus material consisted of 24 abstract nouns and 72 pronounceable non-words. The nouns consisted of four- and five-letter words, and were matched for neighbourhood frequency ($=2$). The CELEX frequency values ranged from 7.15 to 76.20 ($m = 38.07$, $SD = 24.47$). Each word was matched with a non-word of the same length. The remaining non-words were matched to result in an additional set of non-word pairs. The word pairs were displayed in black (33 point Courier New Bold font) against a grey background on the computer screen (see Figure 1). Each letter string was presented with their centre 25 mm from central fixation (visual eccentricity: 2.5 degrees of visual angle per half-field). In each trial, we presented a fixation cross for 1000 ms before the word pair was shown for 150 ms, followed by a blank screen until a response was given (Figure 1). Participants were instructed to indicate whether they saw a meaningful English word on the left or right, or did not see a meaningful English word at all. To do so, participants had to press the shift key ipsilateral to the word with the index finger or space bar with both thumbs if they did not see a meaningful string of letters on the screen. There were two experimental

blocks with 72 trials per block. Each block consisted of three 24-trial conditions (word left/non-word right, non-word left/word right, non-word/non-word). The order of the stimuli was randomised within blocks and between participants. In addition, for the critical trials (in which a word was presented) each word stimulus appeared once in each visual field. Prior to the experimental task each participant undertook a practice block consisting of 10 trials with words not used in the experimental trial. We assessed the number of correct lexical decisions and the mean reaction times for correct lexical decisions for the LVF and RVF separately. Control trials (two non-words were displayed on either side of the screen) requiring a space bar response were not further considered for statistical comparisons.

Figure 1 and Figure 2 about here

Lateralized Facial Decision Task

Participants were presented with facial stimuli against a grey background on the computer screen (see Figure 1). Due to the potential effect of emotional faces on laterality (Workman, Peters, & Taylor, 2000), we selected faces with neutral expressions. More specifically, the original faces used to create whole faces and composite faces (used also here) were photographed in a study in which 294 participants were asked to take a neutral pose before being photographed straight on (study 1 in Penton-Voak, Pound, Little, & Perrett, 2006). Thus, each face appeared as symmetrical as possible with the central plane

of the face in line with the centre of the screen (Figure 2). The eccentricity of each face picture was ~ 4 degrees of visual angle and the pictures were 335 x 400 pixels. This was to ensure that important facial information, such as eyes, nose and mouth, would fall in a similar visual angle as the words in the lexical decision task (~2.5 degrees). The final pictures consisted of 10 male and 10 female facial images (example in Figure 2) that had been used in a previous study (study 2 in Penton-Voak et al., 2006). From these, 20 sexually-dimorphic composite faces were constructed (Figure 2) with an equal amount of female and male half-faces appearing in each visual field. The same 20 composite faces were also presented mirror-reversed resulting in 40 composite faces. In each trial, a black central fixation point was presented on the screen for 1000 ms followed by the stimulus that was displayed for 150 ms. Following presentation of the stimulus, a blank screen was presented until a response was provided (Figure 1). In this task participants had to press the left shift key if the face appeared to be female and the right shift key if the face appeared to be male. There were two experimental blocks with 60 trials per block making 120 trials in total. Prior to these test trials participants were presented with a practice block of 10 trials consisting of two whole faces and eight composite faces that were not included in the experimental trials. We assessed the number and response time of facial decisions towards the LVF and RVF. In the control condition, whole faces were presented (Figure 2).

Data analysis

First, we excluded individual data points that were <150ms and >4000ms. This resulted in the exclusion of 34 data points from 3 younger adults and 10 older adults (range of data points excluded per participant: 1-6) in the lexical decision task and of 26 data points from 3 younger adults and 8 older adults (range of data points excluded per participant: 1-8) in the facial decision task. Subsequently, we excluded individual data points as done by Bermond, Bleys and Stoffels (2005). These authors removed reaction time data for each participant which deviated from each participant's personal mean by more than $\pm 2SD$. These individual responses were considered to reflect a chanced guess on the part of the participant and not an informed decision. Following this criterion, we excluded 237 individual responses from the lateralized lexical decision task (20 older participants: average of 6.3 (SD 2.8) data points removed, range: 2-11 data points; 20 younger participants: average of 5.6 (SD 1.9) points removed, range: 2-11 data points), and 210 individual responses from the facial decision task (20 older participants: average of 4.5 (SD 1.8) data points removed, range: 2-8 data points; 20 younger participants: average of 6.0 (SD 1.8) data points removed, range: 3-10 data points).

In order to assess lateralized performance between visual fields and age groups, while accounting for the possibility of differential sex effects (Hausmann et al., 2003), we performed two separate 2 x 2 x 2 mixed sample ANOVA's with visual field (LVF, RVF) as the related samples factor and age (younger adults vs. older adults) and sex (male vs. female) as the independent samples factors on percent correct responses and reaction

times for correct responses, respectively. Likewise for the facial decision task, to ascertain that participants could distinguish between male and female whole faces, and that percentage of correct sex decisions was higher than the percentage of sex decisions according to the left side of the composite face (left face decisions), we performed a repeated measures ANOVA on percent correct responses for whole faces and percent left face decisions (composite faces) as repeated measures and age (younger adults vs. older adults) and sex (male vs. female) as between subjects measures. For this measure, right face decisions were not accounted for (left face and right face decisions add up to 100%). To also test whether there was a reaction time difference between whole faces and composite faces, and that left face decisions were potentially faster than those for right face decisions (Bourne, 2008), we performed a repeated measures ANOVA on mean reaction times for sex decisions with face type (correct decisions for whole faces, left face decisions, and right face decisions) as repeated measure and age group (younger adults vs. older adults) and sex (male vs. female) as between subjects factors. Finally, to test whether the male and female age groups showed a left face bias at all, we performed one-tailed tests against chance level (50) on percent left face sex decisions for each group separately. For all statistical analyses the α -level was set at .05, unless otherwise stated.

Results

3.2 Lateralized Tasks

3.2.1 Lexical decision task

The ANOVA on accuracy revealed a significant main effect of visual field ($F(1, 36) = 43.400, p < .001$) with performance being superior for RVF (74.38 ± 18.05) than LVF (44.95 ± 23.52) presentations. The main effect of age group was significant ($F(1, 36) = 4.313, p = .045$) with performance being superior in younger (63.75 ± 8.56) than older (55.57 ± 15.62) adults. The main effect for sex was not significant ($F(1, 36) = 0.652, p = .425$). There were significant interactions between visual field and age group ($F(1, 36) = 9.404, p = .004$) and between visual field and sex ($F(1, 36) = 5.493, p = .025$). Post-hoc Tukey comparisons on the first interaction showed a RVF over LVF advantage in younger ($p = .0002$) but not older ($p = .079$) adults. These comparisons also showed that younger adults made more accurate lexical decisions than the older adults for words presented to the RVF ($p = .003$) with an equal performance between groups for words presented to the LVF ($p = .79$) (see Table 1). Post-hoc Tukey comparisons on the second interaction showed a stronger RVF over LVF advantage in male ($p = .0002$) than female ($p = .024$) participants. These comparisons also showed that the sexes performed comparably for LVF ($p = .110$) and RVF ($p = .614$) presentations (see Table 1). The three-way interaction between visual field, sex and age group was not significant ($F(1, 36) = 1.442, p = .238$).

The analogous ANOVA on mean reaction times for correct responses revealed a significant main effect of visual field ($F(1, 36) = 9.443, p = .004$) with individuals responding faster to words presented in the RVF ($626.22\text{ms} \pm 155.36\text{ ms}$) than LVF

(683.84ms \pm 156.58ms). The main effect of sex was also significant ($F(1, 36) = 5.006, p = .032$) with men (590.01ms \pm 122.31ms) responding faster than women (693.94ms \pm 150.35ms). The main effect of age group ($F(1, 36) = 3.324, p = .077$) and the interactions between visual field and age group ($F(1, 36) = .737, p = .396$), between visual field and sex ($F(1, 36) = 2.513, p = .122$), and between visual field, age group and sex ($F(1, 36) = .370, p = .547$) were all not significant (Table 1).

Insert Table 1 about here

3.2.2 Facial Decision Task

The repeated measures ANOVA on percentage accuracy showed a main effect for face type ($F(1,36) = 105.06, p < .001$) indicating that accuracy was higher for whole faces (79.88 \pm 16.98) than was the proportion of decisions according to the left face (58.84 \pm 17.21). There was a main effect of age group ($F(1,36) = 16.89, p < .001$) indicating that the overall percentage of responses (correct decisions for whole faces and left face decisions) was higher for younger (79.38 \pm 10.87) than for older (64.44 \pm 15.82) participants. The main effect of sex ($F(1,36) = 2.296, p = .138$) and the interaction between face type and age group ($F(1, 36) = 3.068, p = .088$) were not significant. The interactions between age group and sex ($F(1, 36) = 16.446, p < .001$), between face type and sex ($F(1, 36) = 25.108, p < .001$), and between face type, age group and sex ($F(1, 36) = 4.743, p = .036$) were significant. Because the two-way interactions are part of the

three-way interaction, we focussed only on the latter. In order to understand this three-way interaction, we performed analogous ANOVAs on age group and sex for the two face types separately. The ANOVA on whole faces showed a significant interaction ($F(1, 36) = 6.778, p = .013$). Tukey post-hoc tests indicated that accuracy was lowest for older men when compared with the performance of all other groups (all p -values $< .001$). The remaining single comparisons were not significant (all p -values $> .350$) (Table 1). The ANOVA on left face decisions showed a significant interaction as well ($F(1, 36) = 18.050, p < .001$). Tukey post-hoc tests indicated that the left face bias was strongest in younger men when compared to the left face bias in both older men ($p < .001$) and younger women ($p = .003$), and as a statistical trend when compared to older women as well ($p = .070$) (see Table 1). The remaining comparisons were not significant (all p -values $> .100$).

The one-sample t -tests against chance level (50%, see data analysis section) provided complementary support for the results from the group comparisons above. A significant left face bias was observed in younger men ($t_9 = 6.800, p < .001$), but no bias for left face decisions was observed in older women ($t_9 = 1.629, p = .138$), older men ($t_9 = -1.718, p = .120$), and younger women ($t_9 = 0.560, p = .589$) (Table 1).

The repeated measures ANOVA on mean reaction times showed a main effect of face type ($F(2, 72) = 32.685, p = .001$). Post-hoc Tukey comparisons indicated that reaction

times were faster for whole face decisions (572.59 ± 160.97) than for left face decisions (617.36 ± 192.36 , $p < .001$) and right face decisions (658.45 ± 216.51 , $p < .001$). In addition, left face decisions were faster than right face decisions ($p < .001$). There was a significant main effect of age group ($F(1, 36) = 7.537$, $p = .009$) indicating that older adults (429.33 ± 224.39) responded faster than younger adults (586.48 ± 133.84 , Table 1). The interaction between age group and sex was also significant ($F(1, 36) = 4.788$, $p = .035$). Post-hoc Tukey comparisons showed that older male responded faster than younger female ($p = .020$), younger male ($p = .007$), and at the statistical threshold also as older female ($p = .052$). The remaining comparisons were not significant (all p -values $> .800$; Table 1). The main effect of sex ($F(1, 36) = 2.569$, $p = .118$), and the interactions between face type and sex ($F(2, 72) = 0.652$, $p = .524$), face type and age group ($F(2, 72) = 2.808$, $p = .067$), and between face type, age group and sex ($F(2, 72) = 1.874$, $p = .161$) were all not significant.

Correlations between lateralized tasks

In case that the left and right hemisphere tasks do interact, one could expect that accuracy in one task does relate to accuracy in the other task. The same could be assumed for reaction time measures. Using Pearson correlations, we found that LVF accuracy in the lateralized lexical decision task was unrelated to whole face decisions ($r = -.024$, $p = .885$) and left face decisions ($r = .021$, $p = .896$). RVF accuracy was unrelated to left face decisions ($r = .243$, $p = .131$), but correlated positively with whole face decisions ($r =$

.326, $p = .040$). Analogous comparisons for reaction time measures (including reaction times for right face decisions) were all not significant (p -values $> .180$).

Discussion

In a mixed design, we tested whether performance of older and younger adults in a left hemisphere asymmetry task (lateralized lexical decision task) and a right hemisphere asymmetry task (sex decisions for chimeric faces) would rather support the RHAM or HAROLD model. Irrespective of participants' age and sex, we replicated previous studies that lexical decisions are more accurate and faster when letter strings are presented to the RVF as compared to the LVF (Dutta & Mandal, 2002; Herzig et al., 2010; Leiber, 1976; Mohr, Krummenacher et al., 2005). We also replicated previous studies on lateralized visual face biases such that information of the left half-face is favoured over the information of the right half-face (Butler & Harvey, 2006; Dutta & Mandal, 2002; Herzig et al., 2010). With regard to the most important lateralized findings to the present study, we found a reduced RVF advantage for lexical decision accuracy in older as compared to younger adults. Findings on lateralized performance in the facial decision task were less clear-cut, i.e. these were influenced by both age and sex. In more detail, the commonly observed left face bias was indeed evident in younger men, and was in magnitude more pronounced to the one in older men, but also more pronounced to the one in younger women. Taken together, findings from both tasks would rather support the HAROLD

model (Cabeza, 2002) than the RHAM (Albert & Moss, 1988; Brown & Jaffe, 1975), at least when considering men's performances.

Support for the HAROLD model rather than the RHAM

According to the RHAM (Albert & Moss, 1988; Brown & Jaffe, 1975), age-related cognitive decline should be more pronounced for functions of the right hemisphere (e.g. spatial processing, visual face processing) due to a smaller gray/white matter ratio in the right than the left hemisphere (Good et al., 2001; Gur et al., 1980; Pujol et al., 2002; but see Smeets et al., 2010). Early behavioural data for the RHAM model were reported by Goldstein and Shelly (1981). These authors used results from a neuropsychological test battery assessed in six different age groups ($n = 1247$) to infer that older as compared to younger individuals fared worse overall, but that the performance decline was more pronounced for right than left hemisphere advantage tasks (see also Hommet et al., 2008). Assessing hemispheric advantages more directly using lateralized hemi-field paradigms (Bourne, 2006; Hunter & Brysbaert, 2008), support for the RHAM was inferred from lateralized letter matching tasks of different complexity (20 older adults, 30 younger adults; Cherry et al., 2005), left ear digit recall performance in a dichotic listening paradigm (120 individuals separated into four age groups; Clark & Knowles, 1973), and a lateralized object discrimination paradigm (16 younger adults, 16 older adults; Gerhardstein et al., 1998).

Yet, independent studies, also using divided half-field paradigms, would infer that their results support the HAROLD model (Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz et al., 1999; Smith-Conway et al., 2012). This latter model assumes a more bilateral pattern of hemispheric functioning in older as compared to younger adults due to functional compensation of the contralateral hemisphere assisting the normally superior hemisphere during a given task (see Cabeza, 2002; Hommet et al., 2008 for overviews). For instance, a lateralized letter matching task in 24 older and 24 younger adults (Reuter-Lorenz et al., 1999) pointed to a bilateral visual field advantage for all levels of complexity in older adults, while a bilateral advantage was only observed for medium and high complexity in younger adults (see also Banich, 1998; Reuter-Lorenz & Cappell, 2008). Because we found an attenuated asymmetry when testing healthy participants' performance in two lateralized tachistoscopic tasks, i.e. a right and left hemisphere asymmetry task, we feel encouraged concluding that hemispheric asymmetry is not simply attenuated for the right hemisphere, but that hemispheric symmetry is enhanced in older as compared to younger adults, and that this was most consistently the case for older men. This conclusion would support the HAROLD model (Cabeza, 2002).

Before discussing the role of sex more thoroughly, we would like to acknowledge results from additional hemifield studies i) targeting only right hemisphere advantages in different age groups (although these cannot contrast the RHAM and HAROLD models) and ii) that neither supported the RHAM nor the HAROLD model. For instance, older as

compared to younger adults showed reduced left face biases in a facial decision task (chimeric face task in 22 younger adults and 14 older adults: Butler & Harvey, 2008; chimeric face task in 107 individuals separated into four age groups: Failla, Sheppard, & Bradshaw, 2003). Others, however, failed to observe this reduced left face bias in older individuals (chimeric face task in 20 younger and 20 older adults: Cherry, Hellige, & McDowd, 1995; chimeric face task in 90 women separated into three age groups: Moreno, Borod, Welkowitz, & Alpert, 1990). Most studies used emotional chimeres which might compromise the appropriateness of the stimulus material and the respective conclusions, because hemispheres are differently specialized for different emotions (e.g. Borod, 1992; Borod, Zgaljardic, Tabert, & Koff, 2001; Eviatar & Zaidel, 1991; Mohr, Michel et al., 2005; Mohr, Rowe, & Crawford, 2008).

Alternatively, results from the latter studies might simply support a series of additional reports on lateralized hemifield studies that hemispheric advantages are comparable for younger and older participants, whether testing 120 men on verbal (left hemisphere advantage) and melodic (right hemisphere advantage) material (Borod & Goodglass, 1980), 64 women in the computation of visual-spatial relations (Hoyer & Rybash, 1992), 96 adults in a letter and a face matching task (Obler et al., 1984), and 20 women and 20 men in a consonant-vowel-consonant nonsense syllables task as well as an object matching task (Cherry et al., 1995). Unfortunately, inconsistencies in the study of hemispheric asymmetry are not new (Efron, 1990). We can only add to this inconsistent

literature by here conjecturing that our own results would largely support the HAROLD model, and that these results were obtained from tasks that have shown complementary results before (Herzig et al., 2010). Yet, it remains to be considered to what extent sex and handedness could play a role when contrasting our own results with those of previous studies.

The influence of sex and handedness on lateralized performance

One study tested a priori the influence of sex on the link between hemispheric asymmetry and age (Hausmann et al., 2003). These authors performed three lateralized tasks in 50 younger (23 males) and 42 older (22 males) adults. Results neither supported the HAROLD model nor the RHAM. In their word comparison task, older participants yielded the expected RVF over LVF advantage (accuracy) to a stronger degree than younger participants (a finding that would support the RHAM). In their lateralized figural comparison task, on the other hand, the authors observed a LVF over RVF advantage in younger men and older women, but not in younger women and older men. Thus, older men again would show evidence supporting the RHAM model, while results from older women would point to a pronounced pattern of commonly observed functional hemispheric asymmetries (left lateralized for language, right lateralized for visual object processing). Unfortunately, no visual field by age interaction was observed in their third task, in which participants decided on whether visual stimuli were faces or distorted faces. Of interest to our findings, these authors found no empirical evidence that would

support the HAROLD model, but found that performance of older men across two tasks would support the RHAM model. In our study, however, the performance of older men across the two tasks would support the HAROLD model.

The comparison of our results with those of Hausmann et al. (2003) already indicates that sex is unlikely to explain different results between studies, because in both studies, half of each age group consisted of men. This conclusion can also be drawn when again looking more closely on some of the studies already detailed above, i.e. the number of men and women in the different age groups cannot explain why some studies found evidence for the RHAM, others for the HAROLD, and others no support for either model. To give a representative example accounting for lateralized face tasks (for which we found a modulation by age and sex), Hausmann et al. (2003) found no modulation by age and sex, Cherry et al. (1995) found no modulation by age and sex (half of each age group consisted of men), and Moreno et al. (1990) found no age modulation in their female sample. When considering lateralized letter matching tasks, one study found evidence for the HAROLD model testing 24 older (12 male) and 24 younger (12 male) adults without accounting for sex in their analysis (Reuter-Lorenz et al., 1999), while another study found evidence for the RHAM model testing 30 younger (15 male) and 20 older (9 male) adults (Cherry et al., 2005), in line with Hausmann et al. (2003). In our sample, however, we found a decreased left hemisphere contribution to lexical decisions in 20 older (10 male) than 20 younger (10 male) participants, findings which refute the RHAM model.

Having looked more closely at such study details makes it very unlikely that sex influenced differences between studies. We also argue that our sample sizes cannot account for the differences, because our sample sizes fell within the range tested in previous studies.

To yet consider additional factors that might account for differences between studies, we elaborate on a person characteristic reported in most studies, i.e. handedness. To again focus on studies we already detailed when accounting for possible sex differences, Hausmann et al. (2003) tested right-handed participants (additional person characteristics were not reported), Cherry et al. (1995) tested right-handed students and former students (alumni), Moreno et al. (1990) tested right-handed women who had at least a ninth-grade education, Reuter-Lorenz et al. (1999) tested healthy right-handed participants recruited through their university subject pool (younger participants) or the local institute of gerontology (older participants), and Cherry et al. (2005) tested mainly right-handed students (younger participants) and local volunteers (older adults). In our study, we matched our younger sample to the older sample, i.e. all were right-handed and none had a university degree. Having elaborated that the previous studies supporting the RHAM, the HAROLD or none of them almost all tested exclusively right-handed participants, we do conclude that handedness is unlikely accounting for the differences between studies.

Another obvious variable that might explain differences between studies concerns the actual tasks employed. This possibility can only be enlightened by future studies using tasks that have been used before. Thus, the only conclusion we can come up with is that we found evidence for the HAROLD model, at least in men, using a lateralized lexical decision task and a facial sex decision task on composite faces. These tasks have been used before showing complementary results (Herzig et al., 2010). To what extent the current findings will be more reliable than those of other studies remains to be seen. Hopefully, future studies will use comparable paradigms to facilitate comparison between studies, and to disentangle additional variables that could explain differences between studies.

Limitations

There are several study limitations we would like to acknowledge. Firstly, one obvious limitation concerns the sample sizes tested. Larger sample sizes would certainly provide more reliable findings. This limitation concerns not only our own study, but also previous studies testing comparable sample sizes. Secondly, we did not test for mild cognitive impairments in our older adults, but relied on the home officer's information on the older adults. A short assessment of overall cognitive functioning would benefit a better description of non-student samples. Thirdly, we assessed lateralized performance using two tasks we used before (Herzig et al., 2010). Unfortunately, these tasks are based on different response requirements. Once, individuals make decisions on whether and where

they saw a meaningful word or not, and once they decide on the sex of the presented faces. These response modes and requirements are not directly comparable complicating direct comparisons of task performances. Fourthly, we followed the reasoning of previous authors assuming that lateralized or rather less lateralized performance in older individuals is related to cognitive decline (see introduction, see also Cabeza, 2002; Cherry et al., 2005; Tsujii et al., 2010), but did not test for other cognitive functions. Future studies should assess non-lateralized cognitive functions (see e.g. Powell, Kemp, & Garcia-Finana, 2012 for a very recent example) to investigate whether performance in such tasks relate to functional hemispheric asymmetry. Finally, lateralized performance of younger women might be influenced by hormonal effects varying across the menstrual cycle (Hausmann & Gunturkun, 1999; Heister, Landis, Regard, & Schroeder-Heister, 1989). When younger women are tested randomly, it is highly likely that they are tested during different menstrual cycle phases resulting in some showing lateralized behaviour and others less lateralized behaviour. A potential reduction in lateralized behaviour across a randomly selected group of younger women would enhance the possibility that this group performs similarly to older participants, something we indeed observed in the facial decision task for left face preferences and Hausmann et al. (2003) observed for the figural comparison task. To better control for fluctuating hemispheric asymmetry in younger females across the menstrual cycle, they could be tested around their menses, when their lateralized performance is most comparable to the one of men (Hausmann & Gunturkun, 1999; Heister et al., 1989).

Conclusion

If we do accept that the presently observed attenuation of hemispheric asymmetry may support the HAROLD model, we may also acknowledge its associated assumption: a more bilateral pattern of hemispheric functioning in older as compared to younger adults (in particular men) results from a functional compensation of the contralateral hemisphere assisting the normally superior hemisphere during a given task. It has been argued that the human brain can compensate for age-related changes in anatomy and physiology by reorganizing its functions (Cabeza, 2001; Grady et al., 1994; Hommet et al., 2008; Raz, 2000). Such a compensation might result from brain dynamics comparable to those when hemispheric asymmetry patterns change i) spontaneously over very short periods of time (Mohr, Michel et al., 2005), ii) with changes in hormonal levels (Hausmann & Gunturkun, 1999; Heister et al., 1989), or iii) subsequent to clinical (Regard, Cook, Wieser, & Landis, 1994) or experimentally-induced (Bachtold et al., 2001) hemispheric imbalances. If our attenuated hemispheric asymmetry in older as compared to younger adults results from compensatory or de-differentiation mechanisms (e.g. Dolcos, Rice, & Cabeza, 2002; Hommet et al., 2008), we would expect the respective brain correlates to be found in callosal structures or their connectivities (Regard et al., 1994), because it is likely to be within these structures that dynamic changes in hemispheric asymmetry occur (e.g. Bachtold et al., 2001; Cherry et al., 2005; Hausmann & Gunturkun, 2000; e.g. Regard et al., 1994).

Here, we performed behavioural tasks in a healthy population. As a consequence, the neuronal mechanisms causing the reduced hemispheric asymmetry pattern cannot be specified. Knowing about these mechanisms would, however, be important to understand the implications of any cerebral aging model to those affected. Seemingly, the compensation explanation would assume that energy depletion, cerebral fatigue would result in the dynamic support of the brain correlates of potentially homologous areas of the contralateral hemisphere (Bachtold et al., 2001; Regard et al., 1994; Reuter-Lorenz & Cappell, 2008). On the other hand, proponents of the de-differentiation hypothesis would suggest that the reduction in hemispheric asymmetry in older adults is a reflection of an age-related difficulty in recruiting neural mechanisms specialized for a given task (Li & Lindenberger, 1999).

In sum, we here investigated in a mixed design whether results from a left hemisphere asymmetry task (lateralized lexical decisions) AND a right hemisphere asymmetry task (sex decisions for chimeric faces) would rather support the RHAM or the HAROLD model. Comparing performances of younger and older adults, we obtained support for the HAROLD model, most consistently observed in older men. These findings would indicate that both hemispheres become compromised during the aging process.

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Figure 1: Schematic representation of a trial in the lateralized lexical decision task and facial decision task, consisting of three subsequent events, respectively. The presentation of a fixation cross (Event 1), the presentation of the stimulus for 150ms (Event 2), and a blank screen (Event 3) that remains until a response is provided.

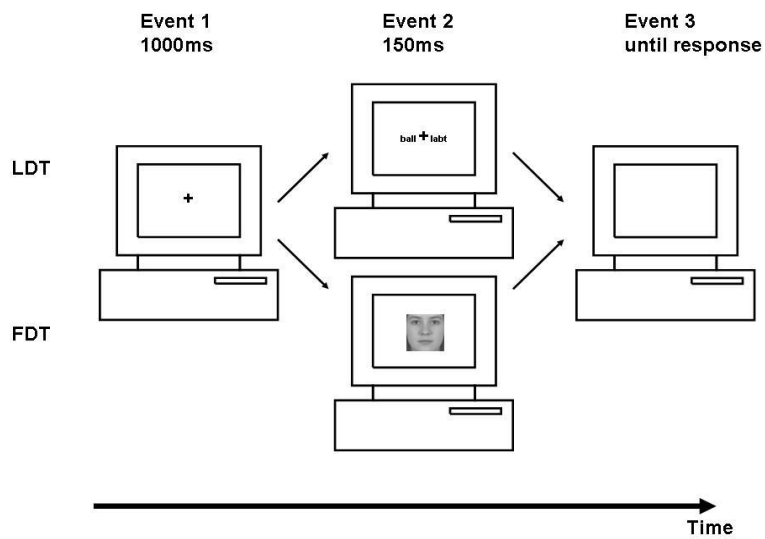


Figure 2: Example of face stimuli used in the facial decision task. Presented is a female face (A), a male face (B), and a chimeric face consisting of a left female half-face and a right male half-face (C)



Table 1: Mean (\pm SD) age, accuracy (in percent) and reaction times (in ms) in the lateralized lexical decision task (LDT) and facial decision task (FDT) of older and younger adults for the sexes separately

	Older Adults	Older Adults	Younger Adults	Younger Adults
	Women	Men	Women	Men
LDT LVF accuracy	54.79 (36.90)	40.63 (12.89)	48.75 (12.58)	35.63 (21.68)
LDT RVF accuracy	65.42 (16.23)	61.46 (17.93)	76.04 (8.41)	94.58 (4.93)
LDT LVF RT	663.12 (161.37)	610.57 (192.03)	770.45 (150.45)	691.24.57 (76.54)
LDT RVF RT	662.72 (136.46)	527.91 (153.19)	715.06 (188.11)	599.19 (72.96)
FDT LF bias	60.25 (19.89)	46.88 (5.75)	52.38 (13.40)	75.88 (12.03)
FDT WF bias	83.50 (10.35)	58.50 (16.04)	91.75 (4.72)	85.75 (12.08)
FDT LF bias RT	643.85 (122.12)	449.52 (254.78)	687.59 (156.98)	688.48 (112.63)
FDT RF bias RT	606.10 (116.94)	421.65 (213.59)	617.76 (131.33)	644.84 (33.27)
FDT WF bias RT	679.69 (134.76)	469.44 (285.18)	710.85 (172.64)	773.80 (125.78)

RVF: right visual field, LVF: left visual field, RT: reaction times, LF: left face, WF: whole face, RF: right face